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The role of cormorants, fishing effort and temperature on the catches per unit effort of fisheries in Finnish coastal areas

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Abstract

Population increase of piscivorous cormorants in Europe and in North America has created a conflict between fisheries and the species. The impact of cormorants on natural fish populations and yields of fishermen is still under debate. We investigated potential connection of the great cormorant *Phalacrocorax carbo* abundance, fishing effort and water temperature with the economically important perch *Perca fluviatilis* and pikeperch *Sander lucioperca* yields, measured as catches per unit of effort (CPUE) in gillnet fishing along the Finnish coastal areas (Baltic Sea) using 50 km International Council for the Exploration of the Sea (ICES) grids. Since cormorants

generally take smaller prey than fishermen, we expected 2–5 years time lag effect of the cormorant numbers on CPUE. Correspondingly, we expected 4–7 years lag effect of temperature on CPUE. Despite the population increase of cormorants, CPUE of perch increased in 10 out of 29 ICES grids during the study period 2005–2014. Pikeperch CPUE increased in five out of 24 grids and decreased in one. There was significant annual variation in CPUE values of perch and pikeperch, but values were not significantly associated with changes in cormorant numbers and temperature either annually or long-term. However, the CPUE values of pikeperch decreased towards the north, which is likely temperature driven as northern colder waters are less suitable for this species than southern waters. There was no clear evidence that either predation by cormorants or fishing effort are associated with long-term trends of perch and pikeperch stocks on a larger scale along the Finnish coast. The increasing CPUE values in several areas indicate that stocks are more abundant than ten years ago despite an increasing cormorant population. Our study approach can be used to monitor potential changes in stocks and impacts of cormorant in the future.

Keywords: cormorant, climate change, fisheries, predator-prey interactions

1. Introduction

Population sizes of the piscivorous great cormorant *Phalacrocorax carbo* and double-crested cormorant *Phalacrocorax auritus* (hereafter together cormorants) have increased strongly in many European countries (great cormorant) and in North America (double-crested cormorant) creating a conflict between fisheries and the species (Carss, 2004; Fielder, 2010a,b; Rudstam et al., 2004; Van Dam and Asbirk, 1997; Veldcamp, 1996). The impact of cormorants on natural fish populations and fish catches is under ongoing debate. Some studies have suggested that cormorant numbers can limit fish stocks (Fielder, 2008, 2010a; Rudstam et al., 2004; Vetemaa et al., 2010) whereas others have found no effect (Dalton et al., 2009; Diana 2010, Diana et al., 2006; Engström, 2001b; Lehikoinen et al., 2011; Östman et al., 2012). Most of these studies concern local cases, and the potential role of cormorants has rarely been investigated on a larger spatial scale.

The great cormorant population in the Baltic Sea has increased strongly in recent decades. On the northern edge of the Baltic Sea, the species bred for the first time in Finland in 1996 (Lehikoinen, 2006) and in 2014 the population consisted of 20,000 pairs. This has been suggested to particularly affect perch *Perca fluviatilis* and pikeperch *Sander lucioperca* populations, which are the two major prey species that have economic importance for fisheries (Lehikoinen, 2005, Mustamäki et al., 2013, Salmi et al., 2015). However, the potential effect of cormorant predation on the catches of the fishermen cannot be distinguished if the effect of environmental variables and fishing itself are not taken into account (Heikinheimo and Lehtonen, 2016; Marzano et al., 2013).

According to cormorant diet studies in the southwestern coastal waters of Finland, perch is an important food object in all studied areas, making up 21–43% of the diet by mass. Contrastingly, pikeperch only appears important for cormorants in the inner archipelago, comprising a 10% share of the diet, as the cormorants mainly take prey species that are abundant in their feeding areas (Salmi et al., 2015). Gillnet fishing is also concentrated in the inner archipelago, increasing especially in the 2000s, as the disturbance by grey seals (*Halichoerus grypus*) has made fishing almost impossible in the outer parts of the archipelago (Heikinheimo and Lehtonen, 2016; Lehtonen and Suuronen, 2004). Most cormorant colonies are situated in the same areas important for commercial coastal fisheries and thus are partly exploiting the same fish resources. As a consequence, effect on fisheries catches could be expected in those areas. However, in the southwestern archipelago, the mortality caused by cormorants on young pikeperch was not higher than 0.04–0.13 (annual instantaneous mortality), which was much less than other natural mortality, at a maximum third of the total mortality in these age groups (Heikinheimo et al., 2016). The cormorant predation mortality on perch has not been studied.

Cormorants generally take smaller prey than fishermen (Lehikoinen et al., 2011; Salmi et al., 2015; Troynikov et al., 2013), which is why there is seldom any direct competition on the same fish individuals. However, if cormorants prey upon substantial amount of fish of the younger age classes, the yields of the fishermen might be affected after a time lag (Salmi et al., 2015). Nevertheless, the mortality effect caused by cormorants may be small if the prey fish stock is dense and the natural mortality from other sources is high (Heikinheimo et al., 2016). Heikinheimo and Lehtonen (2016) have shown in pikeperch that the impact of cormorants on

fisheries catches can be easily overestimated without taking the year class fluctuations and compensatory processes in the fish population into account.

The aim of this study is to investigate how cormorant predation and weather conditions is connected with perch and pikeperch yields, measured as catches per unit of effort in gillnet fishing along the Finnish coastal areas. Climatic conditions, especially temperature, are known to strongly affect the survival of the young-of-the-year of perch and pikeperch (Heikinheimo et al., 2014; Lappalainen et al., 1996, 2000) and this influences the harvests of fishermen after a time lag (Pekcan-Hekim et al., 2011). Our study questions were whether cormorant numbers and water temperature affected the yields of fishermen with a time lag, as a consequence of increased mortality of young fish. We investigated this by examining the change in catch per unit effort (hereafter CPUE) as an index of fish abundance both (i) in the long-term and (ii) annually in a large spatial area. (iii) Third, we investigated, based on population growth rates, how much the cormorant population would still be able to grow in the area. When investigating the potential impact of cormorants on fish stocks, other potential factors such as temperature and fishing effort should be included. Our hypothesis is that cormorant numbers would have a negative effect on fish stocks and therefore we would expect to have decreasing CPUE values in areas with high cormorant densities compared to areas with low cormorant densities. Although our main interest was to investigate the impact of cormorants on fish stocks, it is important to control the potential effect of temperature. Increased temperature improves survival of the young-of-the-year perch and pikeperch and positively affects the yields of fishermen once these age groups have grown to a certain size (Pekcan-Hekim et al., 2011). Last, if fishing effort from the year before is negatively connected with CPUE values, it suggests that harvesting is regulating fish stocks.

Based on our knowledge this topic has not been studied empirically on such a large spatial scale before.

2. Methodology

2.1. Cormorant and fisheries data

The cormorant population of Finland has been intensively monitored along the whole coastline and each of the colonies have been surveyed from the start of colonization using single visit nest counts during the incubation period in May or early June. Since colonies are easy to detect and the species has received a lot of media attention, we are very confident that all of the colonies have been monitored from the start, i.e. since 1996 (see Lehtikoinen, 2006). The most recent monitoring year was 2015 (P. Rusanen, Finnish Environment Institute). Although cormorant numbers have generally increased, there have also been local changes in dynamics and in some areas the population has been declining (Lehtikoinen et al., 2011). This enables comparison between areas with increasing, stable or decreasing cormorant numbers.

The fisheries data consist of catch and effort statistics of commercial gillnet fisheries (36–60 mm bar length) (Pirkko Söderkultalahti, Natural Resources Institute Finland) that are gathered in 50 km grids following the marine regional divisions of the International Council for the Exploration of the Sea (ICES statistical rectangles; Fig. 1a). These data were used to calculate annual catches (kg) per unit of effort (in number of gillnet days), (CPUE) for perch and pikeperch in each ICES statistical rectangle. The gillnet effort, as the number of fishing days, is calculated separately for each species from the catch observations deviating from zero in the reporting period,

which is one month in the coastal fisheries. The CPUE is the catch (kg) of the given species per gear and per fishing day calculated from observations deviating from zero. CPUE is used as an index of fish abundance (Ricker 1975). This assumption is well valid for e.g. net fishing so long as significant gear saturation did not occur (Hilborn and Walters 1992, p. 175). When a single population is being fished, and when effort is proportional to rate of fishing mortality, it is well established that CPUE is proportional to the mean catchable stock present during the time fishing takes place (Ricker 1975). In commercial fishery, the CPUE typically results from thousands of individual units of fishing effort (Hilborn and Walters 1992), such as gillnet days in this case. The Baltic Marine Environment Protection Commission (Helsinki Commission, HELCOM) is for instance commonly using the CPUE values in their core indicators for evaluating the Good Environmental Status of the Baltic Sea (HELCOM 2015). The CPUE values were calculated by dividing the catch with the effort

$$(1) \text{CPUE}_{j,t,i} = \text{Catch}_{j,t,i} / \text{Effort}_{j,t,i},$$

where Catch and Effort are the catch and gillnet effort of the species *j* (perch or pikeperch) in year *t* in grid *i*, respectively. Grids with no gillnet effort targeted on these species were omitted from the analyses. We used unit kg / 100 gillnet days in the analyses. The statistics were available till year 2014, and we used data from the last 10 years (2005–2014) when the cormorant population has been at its highest in the study area. Altogether there are 29 ICES grids along the Finnish coast, but pikeperch is targeted by fishing in only 24 of them because the species is rare in the northern part of the study area and in the outer archipelago (Fig. 1a, Supp. Table 1)

The analyses were conducted using ICES grids (size about 50 x 50 km, but in many grids large parts of the area are not suitable for perch, pikeperch or cormorants due to land area and open deep waters). We calculated the number of breeding cormorant pairs annually in each grid based on the annual locations and sizes of the colonies (P. Rusanen, Finnish Environment Institute). Since cormorants are eating smaller prey than those taken by fisheries (Lehikoinen et al., 2011, Salmi et al., 2015), we used a time lag in the cormorant numbers (mean values of lagged years), when investigating the potential effect of cormorants on catches of fishermen. Depending on growth rate of fish individuals in both perch and pikeperch the fishes preyed upon by cormorants would have mainly reached a suitable size for fishermen after 2 to 5 years (the most common ages of preyed pikeperch and perch 2–5 years; Heikinheimo et al., 2016; Salmi et al., 2015). We thus used the mean number of breeding cormorants in each ICES grid cell 2–5 years prior as a proxy for the effect of the cormorant on the CPUE of a given year.

2.2. Temperature data

We calculated the mean annual summer water temperature for each ICES grid cell using the data provided by the Copernicus, Marine Environment Monitoring Service (myocean.eu). More specifically, we used a database called ‘Baltic Sea Physics Reanalysis from SMHI (1989-2013)’, which provides monthly mean temperatures from a depth of 2 metres throughout the Baltic Sea in 5.5 km grids. We calculated the mean of all grids that were situated inside each ICES grid. In perch we used the period between June and August, based on the monitoring data of Natural Resources Institute Finland, and for pikeperch we used the period July-August (Heikinheimo et

al., 2014; Pekcan-Hekim et al., 2011). Since temperature may affect the survival of 0-year class fishes (Lappalainen et al., 2000), which would recruit to the harvested population after several years, we used temperature data of 4–7 years before the harvest season. This time lag is based on the fact that most pikeperch and perch (females) become large enough in 5–7 and 4–6 years respectively, to be caught by the gillnets of fishermen (Heikinheimo et al., 2016; Pekcan-Hekim et al., 2011; unpublished perch data of the Natural Resources Institute Finland).

2.3. Statistical analyses

2.3.1. Long-term changes

To evaluate how much the cormorant population may yet increase, we investigated the change in annual growth rates of the Finnish cormorant population in relation to the previous year's population size using a linear regression:

$$(2) \ln(N_{t+1}/N_t) \sim N_t,$$

where N is population size in year t or $t+1$.

We tested how changes in $CPUE_{i,j}$ during the time period 2005–2014 were related to changes in the local cormorant population and water temperature in grid i . First, we calculated the average rate of change in $CPUE_{i,j}$, referred as $bCPUE_{i,j}$, using linear regressions between log-transformed $CPUE_{i,j}$ and years (2005–2014). Second, we examined how $bCPUE_{i,j}$ might be explained with grid-specific average rate of

changes in cormorant numbers during 2003–2012, the maximum number of breeding cormorants during 2003–2012, and average rate of change in temperature 2000–2009. Here we used a time lag in cormorant numbers (grid specific log-transformed maximum annual number of breeding pairs during years 2003–2012, two year time lag with the CPUE values). Furthermore, we used a grid specific log-transformed maximum value of breeding cormorant pairs as the maximum value of cormorants in the grid. Correspondingly, we investigated the rate of change in temperatures during summer (see species specific periods above) using a five-year time lag for the CPUE values (2000–2009). Temperature data was not log-transformed. Since trend in cormorant numbers and maximum number of cormorants were strongly correlated ($r = 0.66$), we did not use these two variables in the same model. Our model were thus

$$(3) \text{ bCPUE}_{ij} \sim \text{bCor}_i + \text{bTemp}_i$$

$$(4) \text{ bCPUE}_{ij} \sim \text{Cormax}_i + \text{bTemp}_i$$

where bCPUE is average long-term change in CPUE in species j in grid i , bCor and Cormax are growth rate and log-transformed maximum size of cormorant population in grid i , and bTemp is the rate of change in temperature in grid i . We used the R function lm for the long-term analyses.

2.3.2. Annual variation

Furthermore, we used linear mixed effect models to explain the annual changes in ICES grid specific log-transformed perch and pikeperch CPUE values (function lme of nlme package in program R).

Our explanatory variables were: log-transformed catch per unit effort ($CPUE_{t-1}$), fishing effort year before (Ef_{t-1}), mean temperature (Temp, depending on species 5 to 7 or 4 to 6 years before, see *Temperature data* above), number of breeding cormorants 2 to 5 years before (Cor), latitude coordinate of the grid (Lat), and study year (Year). The equation of the full model was

$$(5) CPUE_{i,t,j} \sim CPUE_{i,t-1,j} + Ef_{i,t-1,j} + Temp_{i,t-lag,j} + Cor_{t-lag,j} + Lat_j + Year + 1 \mid \text{grid},$$

where $CPUE_{i,t,j}$ is catch per unit values of species i , in year t and from grid j . $Ef_{i,t-1,j}$ is the fishing effort of the fish species i one year before ($t-1$). $Temp_{i,t-lag,j}$ is temperature in grid j based on lag and time requirements of species i . $Cor_{t-lag,j}$ is a mean number of breeding cormorants 2–5 years before in grid j and Lat_j is the latitude of the grid. Year is study year as a categorical variable and grid was included as a random factor. The base model included only $CPUE_{i,t-1,j}$ and Year as fixed variables and grid as a random factor. In the annual analyses, we used R function lme of the nlme package.

We used CPUE of the previous year ($CPUE_{i,t-1,j}$) to account for autoregressive dynamics. Furthermore, the effort year before could reveal the impact of fisheries on fish stocks. Negative relationship between CPUE and effort year before could indicate that increasing fishing effort may have caused decreased fish stocks. The fishing effort and the cormorant numbers were log-transformed ($\ln(\text{value} + 1)$) before the analyses because of large variation in the magnitude of the cormorant numbers. Since the fishing effort and temperature were strongly negatively correlated with the latitude we transformed temperature into ICES grid specific temperature anomalies (mean 0 within each grid), as we were interested in the effect within each grid annually.

Furthermore, there was still strong negative collinearity between cormorant numbers and latitude (-0.46 and -0.50 for perch and pikeperch, respectively, both of which are close to the recommendations given by Booth et al. (1994); $|r| < 0.5$). We did not standardize cormorant values, since we need the non-standardized values to test if spatial differences in cormorant population size are associated with CPUE. Instead, we avoided using cormorant numbers and latitude in the same model. Otherwise the correlation between variables was lower, $|r| < 0.42$.

We tested the connection between fishing effort, temperature, cormorants and latitude with CPUE values separately for perch and pikeperch. We used Akaike information criteria to do the model selection (Burnham & Anderson, 2002). We did not consider models within 2 AIC units of each other or the top model, but included uninformative parameter(s) (*sensu* Arnold, 2010).

All the analyses were conducted in R version 3.3.1 (R Core Team, 2016).

3. Results

3.1. Change in cormorant numbers

The Finnish cormorant population consisted of c. 23,000 pairs in 2015. The annual population growth rates of cormorant have strongly declined during last 15 years (Fig. 2) and the population is mainly concentrated to the western and southern sea areas (Fig. 1b). There are no colonies around inland lakes in Finland.

3.2. Long-term changes in CPUE

For perch average long-term change in CPUE were significantly positive in 10 out of 29 ICES grids during 2005–2014, whereas significantly negative trends were not found in any of grids. Correspondingly, in pikeperch significantly increasing trends were found in five grids out of 24 and a significant decreasing trend was found in one grid (Suppl. Table 2; Fig. 1a). Grid-specific trends in temperature and cormorant numbers or the maximum size of cormorant population were not significantly connected with the average long-term change in CPUE in the corresponding grids either in perch or pikeperch (Table 1; Fig. 3). The significant intercepts in the both perch models and in one out of the two pikeperch models suggested generally average long-term increase in the CPUE values (Table 1).

3.3. Annual variation in CPUE

In perch, none of the models were clearly better than the base model, which included $CPUE_{t-1}$ and year (AICc difference less than 2; Table 2). Thus, only the base model was considered. CPUE values were positively connected with CPUE values year before suggesting positive autocorrelation (Table 3). Furthermore, CPUE values showed significant annual variation. More specifically, year 2009 had significantly lower and year 2014 significantly higher CPUEs than the starting year (2005), but other years did not significantly differ from that first year (Table 3).

In pikeperch, the top ranked model included CPUE year before, latitude and year, and was clearly better than the base model (Table 4). There were three other models within 2 $\Delta AICc$ (Table 4), but all these included the same variables as in the top ranked models and additional variables in these models can be considered as

uninformative parameter(s) (Arnolds 2010). Thus, we only considered the top ranked model. Based on the coefficients, CPUE values of pikeperch were significantly negatively associated with latitude and significantly positively connected with CPUE values year before suggesting positive autocorrelation (Table 5, Fig. 4).

4. Discussion

Our findings show that the average long-term changes in CPUE were mainly non-significant or positive in perch and pikeperch in ICES grids along the coastal waters of Finland. Furthermore, despite significant annual variation in CPUE values, we did not find any evidence that CPUE values would have been negatively associated with cormorant numbers or fishing effort in the year prior. In addition, there is a clear latitudinal gradient in pikeperch, with CPUE values being larger in the south compared to northern latitudes (see also Pekcan-Hekim et al., 2011). Although our results could not detect any connection between temperature and CPUE values, this gradient is likely climate driven (Lappalainen et al. 1996, 2000).

According to our results average long-term changes in CPUE of perch and pikeperch show more increasing than decreasing trends during 2005–2014. As the CPUE is considered an index of fish abundance (Ricker 1975), this suggests that fished stocks of these species have generally increased. Pikeperch CPUE levels have remained relatively stable for decades, except for a temporary peak in 1990s (Pekcan-Hekim et al., 2011). We are not aware of any temporal change in the efficiency of gears during the study period. In addition, the gillnet material has been the same during the study period. Recent changes in CPUE values could be also climate driven as warmer waters in the northern Baltic Sea are expected to cause an increase in

warm-adapted and freshwater species (Mackenzie et al., 2007) such as perch and pikeperch (Lappalainen et al., 1996). We did not find any evidence that changes in cormorant numbers are linked with change in CPUE, either annually or with long-term average changes. Furthermore, the CPUE trend analyses showed that CPUE values have significantly increased in several ICES grids, but decreased in only one grid in pikeperch. This suggests that despite increasing cormorant populations, fishable stocks of perch and pikeperch are abundant on a larger scale. The result is in concordance with the finding by Heikinheimo et al. (2016) that the mortality of pikeperch caused by cormorants in the Archipelago Sea was low compared to the level of natural mortality from other sources. Also, Heikinheimo and Lehtonen (2016) found no change in the mortality of perch in the same area when the periods before and after the establishment of the cormorant population were compared. If cormorants have an effect on fished populations, it might be more local and cannot be captured with the 50 km grid resolution. Although our survey grids are relatively large, they are currently the smallest unit where CPUE values can be examined on a larger scale. Furthermore, cormorants are relatively mobile (mean foraging distance 5 km) and their feeding area regularly extends up to 25 km from the breeding colonies (Thaxter et al., 2012). Importantly, our study design covers areas with high cormorant population densities also in European scale (see Bregnballe et al., 2014) as well as areas with no cormorants. This should enhance the potential to detect potential connections between cormorant numbers and changes in fish stocks.

Mustamäki et al. (2014) deduced that pikeperch year class strength, based on CPUEs of three-year-old pikeperch in experimental gillnet fishing, was negatively affected by the presence of cormorants in a coastal area of Sweden, but such a trend was not seen in the commercial catches. Although cormorants consume relatively

large number of fishes, they typically take smaller fish than commercial fisheries (Lehikoinen et al., 2011, Salmi et al., 2015). As the mortality of young age groups is generally high, a large part of the cormorant predation may not be additive to other mortality (Hilborn and Walters, 1992; Heikinheimo et al., 2016). Compensatory mechanisms such as density-dependent mortality and growth (Rose et al., 2001; Heikinheimo et al. 2016) counteract the effect of predation mortality on fisheries catches. Despite this, there are local studies which indicate that e.g. perch populations can be less dense near cormorant colonies, however it is not known whether is this due to predation or indirect effects such as changes in water quality and vegetation, or avoidance of areas with higher predation risk (Gagnon et al., 2015).

With perch, one explanation to the missing connection between cormorant abundance and fisheries CPUEs is that cormorants eat both small sized males and females, but it is mainly females that grow large enough to be caught by fishermen (Heikinheimo and Lehtonen, 2016). Therefore, assuming that all perch taken by cormorants would have grown to the sizes caught with gillnets leads to overestimate of potential catch losses (Salmi et al. 2015; Heikinheimo and Lehtonen, 2016).

Not only are cormorants mobile, but some fish are moving too, whereas some are quite sedentary. The range of migration usually depends on the distribution of food resources, the temperature conditions and abundance of neighbouring populations, as well as the morphology of the archipelago (Aro, 1989). For example, the migrations of perch are shorter in areas where the archipelago zone is narrow. When the area of shallow archipelago is extensive, the migrations are longer. About half of the recaptures of tagged perch in Finnish coastal waters are made at a distance of about 20 km from the point of release (Böhling and Lehtonen, 1984). The dispersal area of tagged pikeperch was also small in areas where the tagging site was

394 surrounded by a sparse archipelago. Locations where the dispersal area was large
395 usually had good connections with other archipelagos. In most cases, 75% of
396 pikeperch recaptures were made within a distance of 10 km from the tagging point
397 (Lehtonen and Toivonen, 1987). Since the dispersal distances seem to me relatively
398 short, the CPUE values of the grids are less likely driven by mixing of several grids.

399 Lappalainen et al. (1996, 2000) have shown that survival of zero-year-old perch
400 and pikeperch is higher in warmer temperatures, which explains the latitudinal
401 pattern. It is possible that our study period was not long enough to catch this climatic
402 effect, as especially in pikeperch CPUE peak years caused by the climatic fluctuation
403 are scarce (Pekcan-Hekim et al., 2011), but temperature is still the main factor
404 explaining the year-class strength in pikeperch (Heikinheimo et al. 2014). In addition,
405 temperature data from the whole grid cell may not necessarily reflect the conditions
406 experienced by young-of-the-year perch and pikeperch as spawning typically occurs
407 in shallow waters (Lehtonen et al., 1996; Snickars et al., 2005; Veneranta et al.,
408 2011).

409 We found no clear evidence that fishing effort in the year prior predicts CPUE
410 values. This may be due to the fact that there were no large changes in the effort
411 during the study period. Commercial fishing with gillnets has been intense in the
412 2000s compared to earlier decades (Pekcan-Hekim et al., 2011). Due to the increased
413 disturbance caused by grey seals (Lehtonen and Suuronen, 2004) in many coastal
414 areas in the 2000s, gillnet fishing has largely moved from the outer archipelago nearer
415 to the coast to more sheltered bay areas, where the fishing effort directed to perch and
416 pikeperch has increased. Accordingly, in the outer archipelago the gillnet effort has
417 decreased. Perch and especially pikeperch are relatively rare in the diet of grey seals
418 in the Baltic (4% and <1% in the diet according to Lundström et al., 2010,

respectively; in the Finnish study <10% together; Kauhala et al., 2010), and thus seal predation is unlikely any important driver of the perch and pikeperch stocks.

Our population growth models of cormorants suggest that the cormorant population growth rate has been slowing down in recent years. The Finnish cormorant densities start to be at the same level as in other Baltic countries, where saturation has been reached already earlier (Bregnballe et al., 2014). If the Finnish population approaches its saturation point, it is unlikely that the cormorant population will cause large-scale declines in perch and pikeperch populations. Nevertheless, this issue should be monitored on a regular basis as the carrying capacity could alter due to changes in environment, such as climate. We believe that our study design provides an appropriate tool to (i) monitor the changes in perch and pikeperch stocks targeted by commercial fishery in the Finnish coastal waters and (ii) examine potential large-scale connections between cormorants and catchable fish stocks, and the analysis could be applied to other areas where similar monitoring is occurring. However, there is likely a need to investigate potential impacts of cormorants on a more local scale. Since the Baltic Sea and its fish community has been predicted to change due to various environmental drivers, not least to climate change (Andersson et al., 2015; Mackenzie et al., 2007; Pekcan-Hekim et al., 2011; Vuorinen et al., 2015), it is important to continue monitoring fish stocks as accurately as possible.

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611 Table 1. Coefficients of variables (model 3: trends in temperature and log-
612 transformed cormorants numbers, model 4: trends in temperature and log-transformed
613 maximum cormorant numbers) explaining the log-transformed long-term change in
614 CPUE values in perch and pikeperch. Significant test-values are bolded.

	Perch			Pikeperch		
Model 3	B ± SE	t	P	B ± SE	t	P
Intercept	0.042 ± 0.016	2.56	0.017	0.049 ± 0.033	1.47	0.157
Temperature	0.040 ± 0.308	0.13	0.898	-0.549 ± 0.624	-0.88	0.388
Cormorant trend	-0.037 ± 0.045	-0.83	0.415	-0.012 ± 0.061	-0.30	0.771
Model 4						
Variable	B ± SE	t	P	B ± SE	t	P
Intercept	0.052 ± 0.018	2.83	0.009	0.078 ± 0.037	2.11	0.047
Temperature	0.071 ± 0.302	0.24	0.814	-0.530 ± 0.597	-0.89	0.385
Cormorant max	-0.005 ± 0.003	-1.38	0.180	-0.007 ± 0.005	-1.42	0.170

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619 Table 2. Number of parameters (K), AIC differences corrected for a small sample size
620 (ΔAIC_c), and AIC weights of models explaining the annual log-transformed CPUE
621 values of perch in ICES grids on the Finnish coast. $CPUE_{t-1}$ = CPUE of the last year,
622 Cor = number of cormorants, Ef_{t-1} = catch effort year before, Lat = latitude and Temp
623 = temperature. See more detailed in the text.

Model	K	ΔAIC_c	w
$CPUE_{t-1} + \text{Year}$	13	0.00	0.22
$CPUE_{t-1} + \text{Lat} + \text{Year}$	14	0.16	0.21
$CPUE_{t-1} + \text{Cor} + \text{Year}$	14	1.30	0.12
$CPUE_{t-1} + \text{Temp} + \text{Year}$	14	2.08	0.08
$CPUE_{t-1} + Ef_{t-1} + \text{Year}$	14	2.10	0.08
$CPUE_{t-1} + \text{Lat} + \text{Temp} + \text{Year}$	15	2.27	0.07
$CPUE_{t-1} + Ef_{t-1} + \text{Lat} + \text{Year}$	15	2.27	0.07
$CPUE_{t-1} + \text{Temp} + \text{Cor} + \text{Year}$	15	3.40	0.04
$CPUE_{t-1} + Ef_{t-1} + \text{Cor} + \text{Year}$	15	3.44	0.04
$CPUE_{t-1} + Ef_{t-1} + \text{Temp} + \text{Year}$	15	4.19	0.03
$CPUE_{t-1} + Ef_{t-1} + \text{Lat} + \text{Temp} + \text{Year}$	16	4.39	0.03
$CPUE_{t-1} + Ef_{t-1} + \text{Temp} + \text{Cor} + \text{Year}$	16	5.55	0.01

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629 Table 3. Coefficients of variables after model averaging explaining the annual
630 variation in log-transformed CPUE of perch in ICES grids on the Finnish coast.
631 Coefficients that significantly differ from zero are bolded. CPUE_{t-1} is log-transformed
632 CPUE year before.

Variable	B ± SE	Df	t-value	P-value
(Intercept)	2.01 ± 0.18	1,251	10.90	< 0.001
CPUE _{t-1}	0.24 ± 0.06	1,251	4.15	< 0.001
Year 2006	0.02 ± 0.10	1,251	0.18	0.858
Year 2007	0.04 ± 0.10	1,251	0.45	0.655
Year 2008	0.05 ± 0.10	1,251	0.56	0.577
Year 2009	-0.23 ± 0.10	1,251	-2.38	0.018
Year 2010	0.01 ± 0.09	1,251	0.09	0.926
Year 2011	0.13 ± 0.10	1,251	1.38	0.169
Year 2012	0.19 ± 0.10	1,251	1.97	0.051
Year 2013	0.15 ± 0.10	1,251	1.48	0.141
Year 2014	0.27 ± 0.10	1,251	2.72	0.007

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635 Table 4. Number of parameters (K), AIC differences corrected for a small sample size
636 ($\Delta AICc$), and AIC weights (w) of models explaining the annual log-transformed
637 CPUE values of pikeperch in ICES grids on the Finnish coast. Cor = number of
638 cormorants, Eft-1 = gillnet effort year before, Lat = latitude and Temp = temperature.
639 See more detailed in the text.

Model	K	$\Delta AICc$	w
CPUE _{t-1} + Lat + Year	14	0.00	0.31
CPUE _{t-1} + Lat + Temp + Year	15	0.00	0.31
CPUE _{t-1} + Ef _{t-1} + Lat + Year	15	0.96	0.19
CPUE _{t-1} + Ef _{t-1} + Lat + Temp + Year	16	0.99	0.19
CPUE _{t-1} + Temp + Year	14	23.29	0.00
CPUE _{t-1} + Year	13	23.32	0.00
CPUE _{t-1} + Ef _{t-1} + Year	14	23.55	0.00
CPUE _{t-1} + Ef _{t-1} + Temp + Year	15	23.59	0.00
CPUE _{t-1} + Cor + Year	14	25.17	0.00
CPUE _{t-1} + Temp + Cor + Year	15	25.26	0.00
CPUE _{t-1} + Ef _{t-1} + Cor + Year	15	25.30	0.00
CPUE _{t-1} + Ef _{t-1} + Temp + Cor + Year	16	25.46	0.00

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Table 5. Coefficients and their standard errors of variables from the top ranked model explaining the annual variation in log-transformed CPUE of pikeperch in ICES grids on the Finnish coast. $CPUE_{t-1}$ is the CPUE year before, Latitude is the latitude of the grid cell and different years are compared to the starting year 2005. $CPUE_{t-1}$ is log-transformed CPUE year before.

Variable	B \pm SE	Df	t-value	P-value
(Intercept)	28.20 \pm 4.73	1,226	5.97	< 0.001
$CPUE_{t-1}$	0.19 \pm 0.06	1,226	3.21	0.002
Latitude	-0.43 \pm 0.08	1,27	-5.71	< 0.001
Year 2006	0.05 \pm 0.14	1,227	0.35	0.723
Year 2007	-0.09 \pm 0.14	1,227	-0.61	0.545
Year 2008	-0.11 \pm 0.14	1,227	-0.77	0.439
Year 2009	-0.14 \pm 0.14	1,227	-1.00	0.319
Year 2010	-0.05 \pm 0.15	1,227	-0.37	0.715
Year 2011	0.04 \pm 0.14	1,227	0.26	0.796
Year 2012	-0.08 \pm 0.15	1,227	-0.57	0.572
Year 2013	0.11 \pm 0.15	1,227	0.76	0.450
Year 2014	0.22 \pm 0.14	1,227	1.53	0.128

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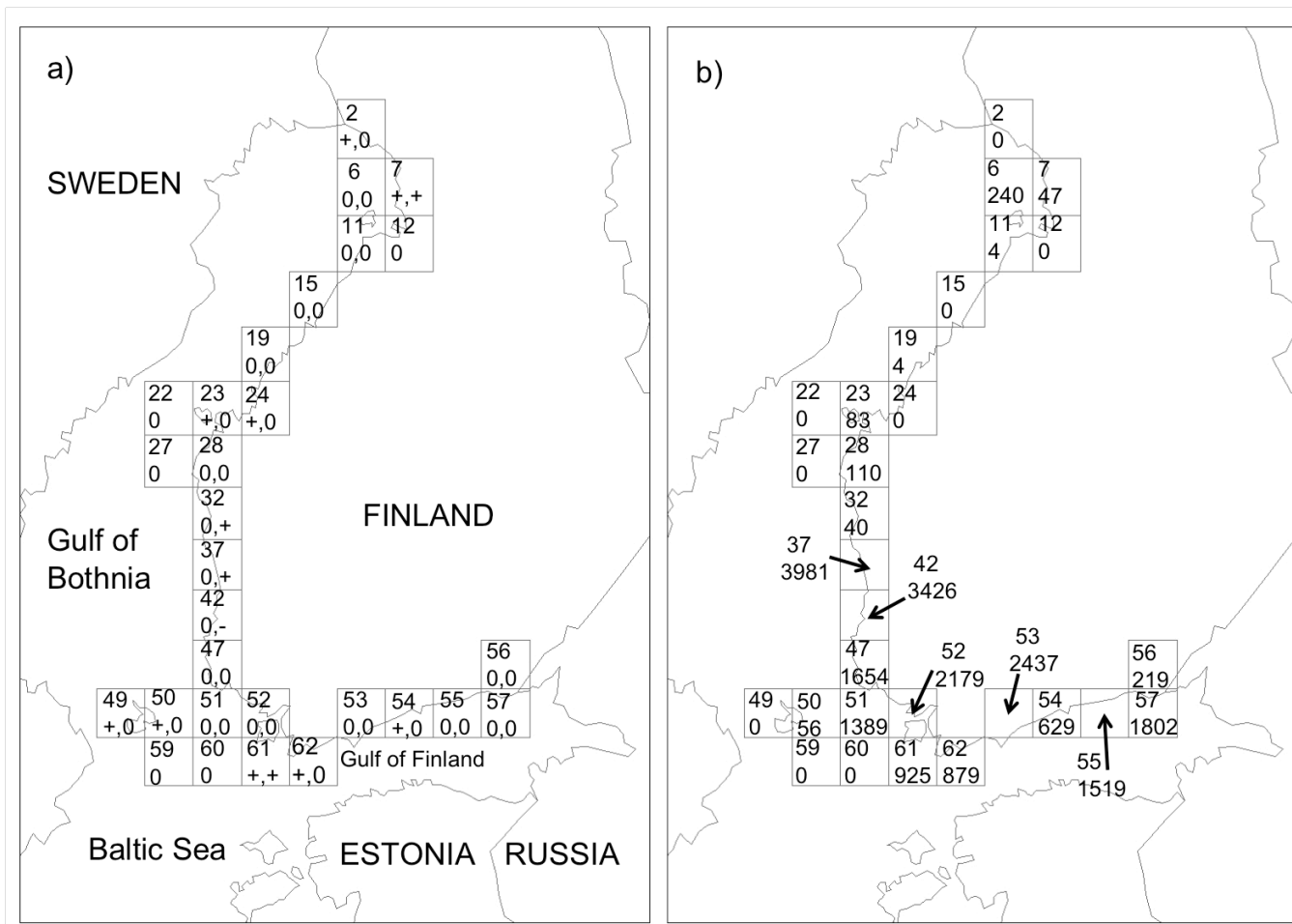
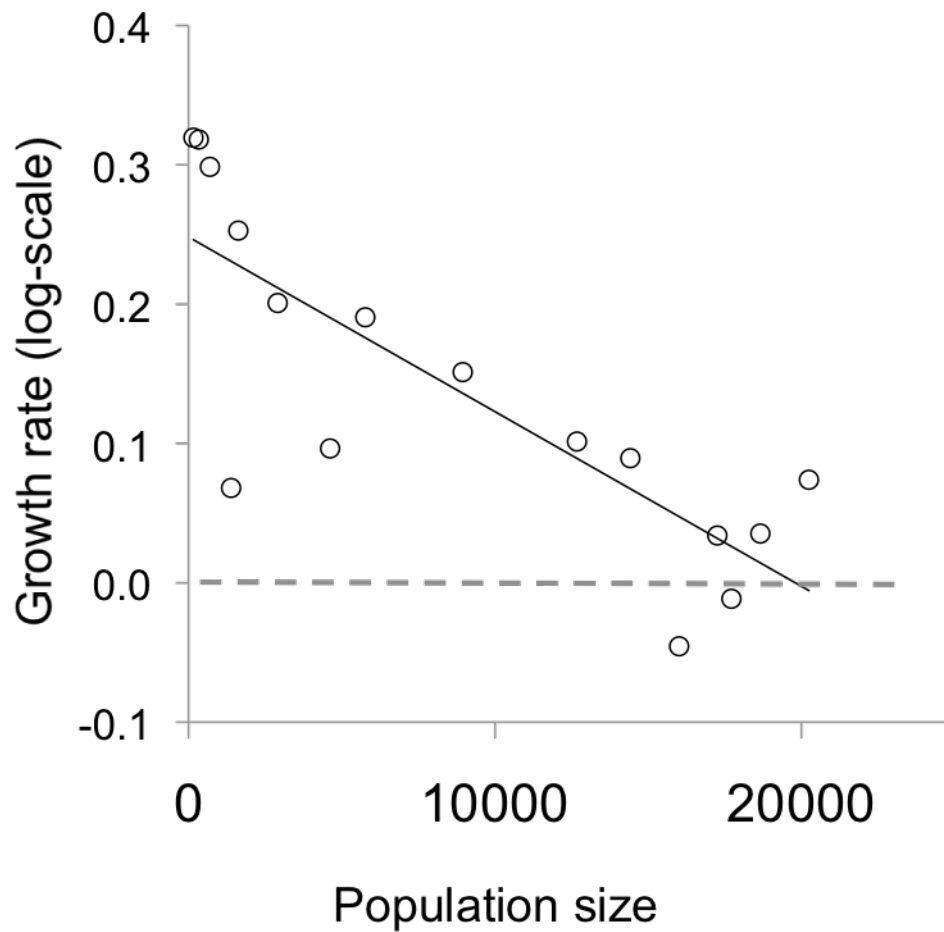
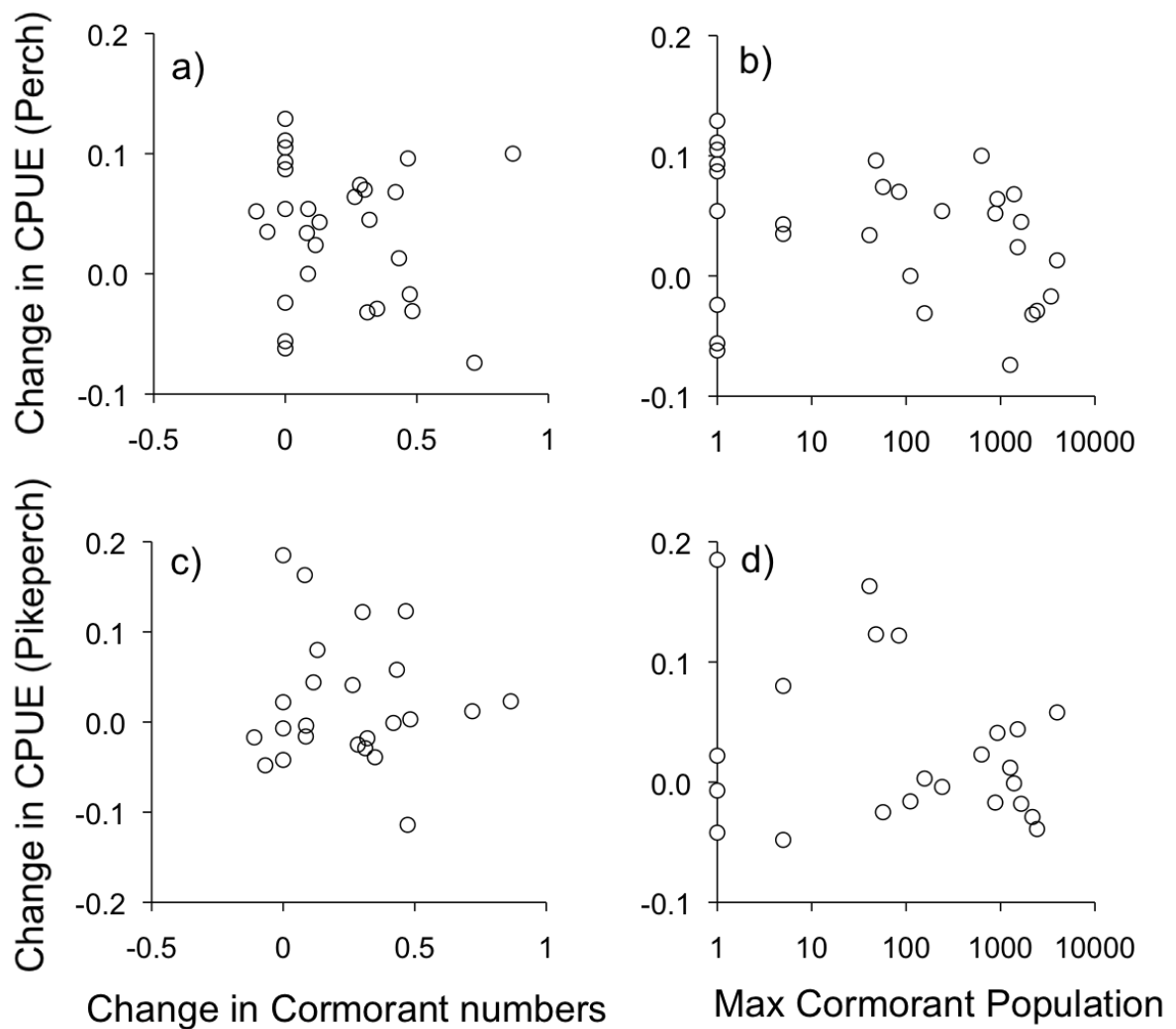


Fig. 1. Study grids along the coastal areas of Finland showing (a) significant changes in CPUE values in perch and pikeperch in 2005–2014 and (b) the maximum number of breeding cormorant pairs in Finland in the northern Baltic Sea inside ICES 50 km grids in 2003–2012 (Table 5). In both panels the upper value is the number of the grid cell, in panel (a) the trends (+ = positive, - = negative, 0 = no significant trend) of perch (left) and pikeperch (right) CPUE are shown below.



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658 Fig. 2. Population growth rate of the Finnish cormorant population ($\log(N_{t+1}/N_t)$) in
659 relation to population size the year before (year t) during 2000–2015. The linear
660 regression line shows the significant negative correlation between variables ($b = -$
661 0.000013 ± 0.000002 , $t = 27.6$, $P < 0.001$).
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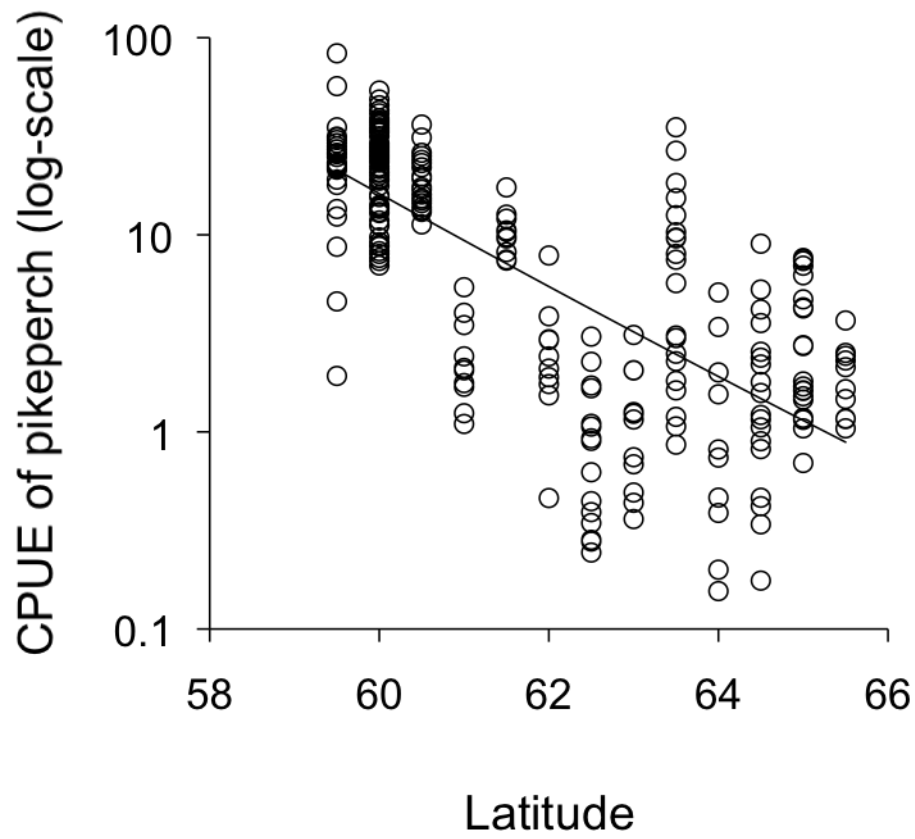


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665 Fig. 3. Annual average change of log-transformed CPUE values (unit kg / 100 gillnet
666 days) in (a-b) perch and (c-d) pikeperch during 2005–2014 in relation to (a and c)
667 population growth rates of log-transformed cormorant numbers and (b and d)
668 maximum population size of cormorants (in log-scale) during 2003–2012 in Finnish
669 ICES grids.

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673 Fig. 4. Annual CPUE values (kg / 100 gillnet days) of pikeperch in relation to latitude
674 on Finnish coasts during 2005–2014.

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678 Supplementary table 1. The data of the analyses including annual grid-specific CPUE

679 values of perch($CPUE_{Perch}$ and $CPUE_{Perch-1}$) and pikeperch ($CPUE_{Pikep}$ and $CPUE_{Pikep-1}$),680 log -transformed fishing effort of perch ($Ef_{Perch-1}$) and pikeperch ($Ef_{Pikep-1}$) year681 before, water temperature for perch (T_{Perch}) and pikeperch (T_{Pikep}), log -transformed

682 abundance of cormorants and the latitude (Lat) of the ICES grids (Grid).

Year	$CPUE_{Perch}$	$CPUE_{Perch-1}$	$CPUE_{Pikep}$	$CPUE_{Pikep-1}$	$Ef_{Perch-1}$	$Ef_{Pikep-1}$	T_{Perch}	T_{Pikep}	Cor	Lat	Grid
2005	4.376	5.719	2.517	5.870	11.055	8.673	0.799	1.060	0.000	65.5	2
2006	3.776	4.376	1.648	2.517	11.079	8.818	0.459	0.820	0.000	65.5	2
2007	6.279	3.776	1.043	1.648	11.253	8.166	0.311	0.140	0.000	65.5	2
2008	6.667	6.279	2.303	1.043	10.681	8.571	0.661	0.680	0.000	65.5	2
2009	9.282	6.667	1.162	2.303	10.299	7.946	0.501	0.730	0.000	65.5	2
2010	7.212	9.282	2.432	1.162	10.508	8.977	0.291	0.650	0.000	65.5	2
2011	9.909	7.212	2.131	2.432	10.467	9.266	0.261	0.510	0.000	65.5	2
2012	10.154	9.909	1.169	2.131	10.584	8.167	0.351	0.460	0.000	65.5	2
2013	8.698	10.154	1.468	1.169	10.089	8.033	0.489	0.520	0.000	65.5	2
2014	12.043	8.698	3.677	1.468	10.534	9.205	0.629	0.740	0.000	65.5	2
2005	11.016	8.776	2.727	3.571	10.748	6.043	0.799	1.041	3.590	65	6
2006	14.956	11.016	1.042	2.727	10.582	6.089	0.429	0.671	4.107	65	6
2007	19.721	14.956	1.151	1.042	10.587	8.302	0.321	0.249	4.410	65	6
2008	15.704	19.721	1.701	1.151	10.547	8.102	0.731	0.769	4.677	65	6
2009	14.619	15.704	0.696	1.701	10.724	8.793	0.511	0.689	4.984	65	6
2010	11.298	14.619	1.179	0.696	10.156	9.079	0.241	0.509	5.127	65	6
2011	14.633	11.298	1.517	1.179	10.441	8.430	0.271	0.479	5.302	65	6
2012	15.181	14.633	1.803	1.517	10.610	7.623	0.391	0.489	5.361	65	6
2013	23.337	15.181	1.458	1.803	10.939	8.803	0.469	0.531	5.281	65	6
2014	25.480	23.337	1.614	1.458	10.647	9.219	0.769	0.941	5.162	65	6
2005	5.868	7.677	2.756	7.328	11.134	9.735	0.749	1.120	0.000	65	7
2006	9.115	5.868	4.706	2.756	11.193	10.328	0.339	0.740	0.000	65	7
2007	9.280	9.115	1.626	4.706	10.971	10.035	0.251	0.110	0.000	65	7
2008	15.557	9.280	4.229	1.626	11.083	10.005	0.541	0.610	0.000	65	7
2009	9.417	15.557	4.288	4.229	11.103	10.013	0.341	0.600	0.000	65	7
2010	13.234	9.417	7.361	4.288	11.278	10.108	0.241	0.610	0.000	65	7
2011	16.603	13.234	7.546	7.361	11.178	9.920	0.391	0.600	1.386	65	7
2012	17.483	16.603	6.970	7.546	11.077	9.445	0.521	0.630	1.792	65	7
2013	15.109	17.483	7.628	6.970	11.127	10.291	0.399	0.440	2.546	65	7
2014	15.282	15.109	6.232	7.628	11.276	10.442	0.799	0.860	3.199	65	7
2005	14.667	14.692	0.340	0.545	10.759	9.273	0.815	1.551	0.000	64.5	11

2006	16.390	14.667	0.176	0.340	10.674	8.083	-	-	0.000	64.5	11
2007	18.813	16.390	1.576	0.176	11.228	7.952	-	-	0.000	64.5	11
2008	8.508	18.813	0.818	1.576	10.729	8.140	0.275	0.171	0.000	64.5	11
2009	8.794	8.508	1.219	0.818	10.954	9.175	0.685	0.399	0.000	64.5	11
2010	9.479	8.794	0.420	1.219	10.900	9.187	0.465	0.339	0.000	64.5	11
2011	18.951	9.479	1.158	0.420	11.004	9.424	0.205	0.169	0.000	64.5	11
2012	22.188	18.951	0.463	1.158	11.033	9.103	0.355	0.219	0.405	64.5	11
2013	21.411	22.188	1.054	0.463	11.217	9.678	0.465	0.239	0.811	64.5	11
2014	17.998	21.411	0.897	1.054	11.195	9.658	-	-	1.179	64.5	11
2005	39.353	8.751	-	-	7.072	-	0.835	1.331	1.179	64.5	11
2006	45.392	39.353	-	-	7.735	-	0.759	-	0.000	64.5	12
2007	24.552	45.392	2.198	0.765	9.512	8.805	-	-	0.000	64.5	12
2008	33.315	24.552	5.278	2.198	10.104	8.174	0.339	-	0.000	64.5	12
2009	35.593	33.315	9.015	5.278	10.400	9.774	0.271	0.130	0.000	64.5	12
2010	19.112	35.593	2.381	9.015	9.841	9.182	0.541	0.660	0.000	64.5	12
2011	33.673	19.112	3.567	2.381	10.217	9.876	0.321	0.630	0.000	64.5	12
2012	40.214	33.673	2.551	3.567	9.923	9.612	0.131	0.540	0.000	64.5	12
2013	20.589	40.214	1.790	2.551	9.937	9.660	0.361	0.560	0.000	64.5	12
2014	18.879	20.589	4.182	1.790	10.243	9.944	0.561	0.670	0.000	64.5	12
2005	2.218	1.546	0.200	0.172	9.305	9.455	-	-	0.000	64	15
2006	5.037	2.218	0.741	0.200	9.326	8.412	0.612	1.102	0.000	64	15
2007	2.392	5.037	0.464	0.741	8.658	4.913	-	-	0.000	64	15
2008	3.800	2.392	0.156	0.464	8.802	6.068	0.578	0.428	0.000	64	15
2009	3.922	3.800	2.004	0.156	9.366	8.075	0.808	0.868	0.000	64	15
2010	4.018	3.922	1.552	2.004	9.811	7.760	0.588	0.728	0.000	64	15
2011	3.757	4.018	0.388	1.552	10.080	8.483	0.028	0.358	0.000	64	15
2012	3.577	3.757	5.099	0.388	10.013	8.884	0.218	0.588	0.000	64	15
2013	2.785	3.577	3.407	5.099	9.519	5.869	0.138	0.428	0.000	64	15
2014	7.622	2.785	0.815	3.407	9.815	6.377	-	-	0.000	64	15
2005	4.039	4.569	12.572	8.153	10.097	9.613	0.962	1.112	0.000	64	15
2006	4.316	4.039	35.125	12.572	9.889	9.766	0.867	1.357	0.000	63.5	19
2007	4.188	4.316	18.321	35.125	10.018	9.638	-	-	0.693	63.5	19
2008	5.629	4.188	7.473	18.321	10.184	9.403	0.417	0.817	0.693	63.5	19
2009	6.611	5.629	10.298	7.473	9.753	9.359	0.303	0.233	0.693	63.5	19
2010	5.211	6.611	8.003	10.298	10.097	9.487	0.703	0.903	0.693	63.5	19
2011	5.577	5.211	26.707	8.003	10.271	9.628	0.553	0.783	0.693	63.5	19
2012	9.312	5.577	9.687	26.707	9.800	9.047	0.023	0.303	0.000	63.5	19
2013	4.642	9.312	15.345	9.687	10.189	9.812	0.413	0.593	0.000	63.5	19
2014	4.757	4.642	9.596	15.345	10.349	9.993	-	-	0.000	63.5	19
2005	9.469	5.031	-	-	7.857	-	0.287	0.317	0.000	63	22
							1.116	-	0.000	63	22

							-					
2006	10.241	9.469	-	-		8.632	-	0.656	-	0.000	63	22
2007	4.709	10.241	-	-		9.493	-	0.284	-	0.000	63	22
2008	15.903	4.709	-	-		9.373	-	0.854	-	0.000	63	22
2009	5.810	15.903	-	-		8.711	-	0.774	-	0.000	63	22
								-				
2010	4.917	5.810	-	-		9.344	-	0.106	-	0.000	63	22
2011	23.995	4.917	-	-		9.711	-	0.234	-	0.000	63	22
2012	5.212	23.995	-	-		8.703	-	0.364	-	0.000	63	22
								-				
2013	21.006	5.212	-	-		6.422	-	0.036	-	0.000	63	22
								-	-			
2014	47.956	21.006	2.050	3.720	8.717	8.322	0.596	0.998	0.000	63	22	
								-	-			
2005	17.660	13.290	0.744	1.127	13.017	11.143	1.086	1.411	0.000	63	23	
								-	-			
2006	17.302	17.660	0.361	0.744	12.956	10.830	0.478	0.841	0.000	63	23	
2007	24.281	17.302	1.261	0.361	13.019	11.091	0.355	0.189	0.000	63	23	
2008	25.204	24.281	1.156	1.261	13.022	10.959	0.932	1.039	0.000	63	23	
2009	19.090	25.204	0.437	1.156	12.897	10.563	0.783	0.889	1.910	63	23	
2010	21.286	19.090	0.685	0.437	13.136	11.195	0.115	0.269	3.258	63	23	
2011	28.047	21.286	1.236	0.685	12.992	10.774	0.453	0.479	3.845	63	23	
2012	30.849	28.047	0.493	1.236	12.931	10.790	0.633	0.509	3.845	63	23	
								-				
2013	30.130	30.849	3.104	0.493	12.921	11.320	0.123	0.211	3.714	63	23	
								-	-			
2014	34.808	30.130	2.057	3.104	12.898	12.001	0.438	0.911	3.534	63	23	
								-	-			
2005	5.287	6.162	2.282	2.232	10.247	9.691	0.707	1.242	0.000	63.5	24	
								-	-			
2006	7.476	5.287	3.085	2.282	11.008	9.529	0.267	0.762	0.000	63.5	24	
2007	5.289	7.476	5.685	3.085	10.518	9.408	0.363	0.268	0.000	63.5	24	
2008	4.701	5.289	1.816	5.685	10.493	9.133	0.583	0.778	0.000	63.5	24	
2009	7.244	4.701	0.862	1.816	10.877	9.706	0.313	0.638	0.000	63.5	24	
								-				
2010	7.937	7.244	1.193	0.862	11.332	10.420	0.107	0.308	0.000	63.5	24	
2011	10.227	7.937	1.067	1.193	11.042	10.140	0.303	0.528	0.000	63.5	24	
2012	12.238	10.227	1.625	1.067	10.342	9.717	0.493	0.628	0.000	63.5	24	
								-	-			
2013	10.304	12.238	2.991	1.625	10.550	9.830	0.227	0.292	0.000	63.5	24	
								-	-			
2014	13.417	10.304	2.492	2.991	10.552	9.523	0.747	0.852	0.000	63.5	24	
								-	-			
2005	13.024	10.619	0.901	0.061	10.228	8.090	1.049	1.270	0.000	62.5	27	
								-				
2006	12.760	13.024	-	-		9.797	-	0.609	-	0.000	62.5	27
2007	24.226	12.760	-	-		9.900	-	0.361	-	0.000	62.5	27
2008	18.266	24.226	1.064	0.140	10.097	6.572	0.881	1.090	0.000	62.5	27	
2009	12.434	18.266	0.244	1.064	10.580	8.207	0.721	0.880	0.000	62.5	27	
								-				
2010	22.884	12.434	0.445	0.244	10.988	9.310	0.149	0.060	0.000	62.5	27	
2011	29.165	22.884	0.283	0.445	10.662	8.593	0.171	0.390	0.000	62.5	27	
2012	24.702	29.165	-	-		10.393	-	0.301	-	0.000	62.5	27
								-				
2013	25.312	24.702	-	-		10.320	-	0.069	-	0.000	62.5	27
								-	-			
2014	32.949	25.312	1.665	0.949	10.135	7.653	0.559	0.960	0.000	62.5	27	

2005	30.679	26.742	1.100	1.163	12.202	10.412	-	-	0.000	62.5	28
							-	-			
2006	27.538	30.679	3.046	1.100	12.096	9.675	0.437	0.716	0.000	62.5	28
2007	28.628	27.538	0.392	3.046	12.402	9.205	0.283	0.284	1.322	62.5	28
2008	29.474	28.628	0.928	0.392	12.196	9.371	0.803	1.014	1.322	62.5	28
2009	21.280	29.474	0.624	0.928	12.272	10.322	0.543	0.804	1.322	62.5	28
							-	-			
2010	20.108	21.280	0.278	0.624	12.744	11.184	0.097	0.214	1.322	62.5	28
2011	28.190	20.108	0.278	0.278	12.839	10.977	0.163	0.404	3.350	62.5	28
2012	25.422	28.190	0.345	0.278	12.792	10.586	0.373	0.424	3.350	62.5	28
							-	-			
2013	24.965	25.422	1.719	0.345	12.716	11.257	0.067	0.216	3.350	62.5	28
							-	-			
2014	35.989	24.965	2.269	1.719	12.867	11.802	0.627	0.876	3.376	62.5	28
							-	-			
2005	26.422	21.060	1.532	2.736	11.482	10.932	0.979	1.448	0.000	62	32
							-	-			
2006	26.139	26.422	1.749	1.532	10.746	9.393	0.369	0.668	0.000	62	32
2007	14.793	26.139	0.462	1.749	11.365	10.703	0.321	0.332	0.000	62	32
2008	27.428	14.793	2.095	0.462	11.402	10.508	0.761	0.962	0.000	62	32
2009	21.887	27.428	2.416	2.095	11.102	10.443	0.411	0.682	0.000	62	32
							-	-			
2010	35.969	21.887	3.861	2.416	11.123	10.812	0.219	0.082	2.398	62	32
2011	33.147	35.969	2.928	3.861	11.239	11.019	0.101	0.372	2.848	62	32
2012	30.720	33.147	1.894	2.928	11.182	10.629	0.421	0.482	2.848	62	32
							-	-			
2013	23.981	30.720	2.953	1.894	11.207	10.843	0.061	0.068	2.848	62	32
							-	-			
2014	31.450	23.981	7.854	2.953	11.262	11.061	0.509	0.728	1.981	62	32
							-	-			
2005	19.331	16.194	7.397	9.213	12.189	12.069	0.904	1.393	3.045	61.5	37
							-	-			
2006	21.389	19.331	9.778	7.397	12.089	11.861	0.294	0.553	4.193	61.5	37
2007	22.013	21.389	10.361	9.778	11.942	11.658	0.366	0.437	5.053	61.5	37
2008	15.251	22.013	7.493	10.361	11.812	11.359	0.676	0.887	5.672	61.5	37
2009	8.426	15.251	8.169	7.493	11.826	11.426	0.296	0.517	6.319	61.5	37
							-	-			
2010	16.597	8.426	12.659	8.169	11.989	11.764	0.404	0.153	6.843	61.5	37
2011	17.775	16.597	12.075	12.659	11.732	11.605	0.056	0.337	7.329	61.5	37
2012	22.244	17.775	10.528	12.075	11.844	11.601	0.456	0.517	7.577	61.5	37
2013	20.125	22.244	9.593	10.528	11.675	11.471	0.156	0.027	7.780	61.5	37
							-	-			
2014	22.467	20.125	17.395	9.593	11.621	11.500	0.404	0.623	7.992	61.5	37
							-	-			
2005	25.192	21.773	4.023	3.465	12.209	11.981	0.836	1.365	1.558	61	42
							-	-			
2006	26.993	25.192	5.420	4.023	12.095	11.727	0.166	0.405	3.618	61	42
2007	21.742	26.993	3.484	5.420	12.298	11.899	0.384	0.455	5.328	61	42
2008	15.845	21.742	1.769	3.484	12.191	11.791	0.714	0.955	6.110	61	42
2009	8.577	15.845	1.244	1.769	12.203	11.684	0.294	0.505	6.609	61	42
							-	-			
2010	14.990	8.577	2.111	1.244	12.117	11.577	0.426	0.175	7.076	61	42
							-	-			
2011	18.179	14.990	2.418	2.111	11.988	11.613	0.006	0.285	7.449	61	42
2012	21.608	18.179	1.097	2.418	11.941	11.355	0.384	0.465	7.697	61	42
							-	-			
2013	18.089	21.608	2.053	1.097	11.718	11.059	0.104	0.045	7.924	61	42

2014	22.860	18.089	1.694	2.053	11.655	10.864	-	-	7.948	61	42
2005	27.544	21.368	36.246	31.384	12.683	12.762	-	-	1.658	60.5	47
2006	24.893	27.544	23.986	36.246	12.751	12.719	-	-	4.047	60.5	47
2007	22.996	24.893	23.122	23.986	12.759	12.779	-	-	4.970	60.5	47
2008	23.790	22.996	22.010	23.122	12.761	12.727	-	-	5.610	60.5	47
2009	12.718	23.790	19.285	22.010	12.634	12.550	-	-	6.251	60.5	47
2010	20.380	12.718	17.424	19.285	12.815	12.797	-	-	6.641	60.5	47
2011	22.625	20.380	31.130	17.424	12.818	12.785	-	-	6.996	60.5	47
2012	24.559	22.625	25.093	31.130	12.742	12.752	-	-	7.115	60.5	47
2013	28.853	24.559	19.820	25.093	12.717	12.696	-	-	7.084	60.5	47
2014	52.489	28.853	26.074	19.820	12.584	12.600	-	-	6.989	60.5	47
2005	36.887	34.006	28.538	37.619	11.567	11.400	-	-	0.000	60	49
2006	41.952	36.887	48.568	28.538	11.478	11.296	-	-	0.000	60	49
2007	44.363	41.952	42.917	48.568	11.333	11.051	-	-	0.000	60	49
2008	47.749	44.363	28.654	42.917	11.300	11.035	-	-	0.000	60	49
2009	47.203	47.749	33.814	28.654	11.251	10.920	-	-	0.000	60	49
2010	71.038	47.203	45.424	33.814	11.093	10.694	-	-	0.000	60	49
2011	78.915	71.038	53.931	45.424	10.982	10.715	-	-	0.000	60	49
2012	92.114	78.915	37.162	53.931	11.310	10.967	-	-	0.000	60	49
2013	62.831	92.114	26.338	37.162	11.226	10.815	-	-	0.000	60	49
2014	71.234	62.831	34.552	26.338	11.386	10.970	-	-	0.000	60	49
2005	27.161	23.152	12.889	21.376	12.149	11.126	-	-	0.000	60	50
2006	38.139	27.161	22.186	12.889	11.975	10.550	-	-	0.000	60	50
2007	35.351	38.139	13.741	22.186	11.914	10.878	-	-	0.000	60	50
2008	32.390	35.351	8.258	13.741	11.926	10.783	-	-	0.000	60	50
2009	22.876	32.390	8.719	8.258	11.794	10.630	-	-	0.000	60	50
2010	32.368	22.876	17.726	8.719	11.593	10.372	-	-	2.442	60	50
2011	42.197	32.368	7.643	17.726	11.404	9.481	-	-	3.239	60	50
2012	57.617	42.197	8.809	7.643	11.759	10.680	-	-	3.239	60	50
2013	50.976	57.617	9.699	8.809	11.447	9.936	-	-	3.239	60	50
2014	56.280	50.976	18.821	9.699	11.470	10.094	-	-	3.114	60	50
2005	28.509	19.050	23.256	27.685	12.161	12.258	-	-	3.229	60	51
2006	35.825	28.509	25.492	23.256	12.119	12.136	-	-	3.555	60	51
2007	30.000	35.825	21.569	25.492	11.838	11.826	-	-	4.252	60	51
2008	24.264	30.000	24.425	21.569	11.668	11.696	-	-	4.670	60	51
2009	13.346	24.264	11.820	24.425	11.396	11.334	-	-	5.215	60	51
2010	23.678	13.346	11.136	11.820	11.387	11.415	-	-	5.745	60	51
2011	29.954	23.678	27.765	11.136	11.306	11.489	-	-	6.187	60	51
2012	37.946	29.954	24.535	27.765	11.588	11.538	-	-	6.305	60	51

2013	53.535	37.946	19.975	24.535	11.464	11.494	0.253	0.018	6.479	60	51
2014	55.925	53.535	24.913	19.975	10.843	10.795	-	-	6.757	60	51
2005	11.848	8.297	31.640	36.156	12.311	12.512	-	-	3.442	60	52
2006	10.031	11.848	36.258	31.640	12.275	12.387	-	-	4.369	60	52
2007	9.828	10.031	37.396	36.258	12.403	12.516	0.322	0.557	5.372	60	52
2008	10.412	9.828	36.166	37.396	12.404	12.473	0.138	0.173	5.878	60	52
2009	6.884	10.412	27.348	36.166	12.186	12.232	0.768	1.083	6.497	60	52
2010	8.520	6.884	24.601	27.348	12.271	12.351	0.398	0.673	6.999	60	52
2011	10.239	8.520	34.714	24.601	12.268	12.387	-	-	7.195	60	52
2012	10.225	10.239	33.586	34.714	12.217	12.361	0.002	0.263	7.339	60	52
2013	7.128	10.225	26.882	33.586	12.201	12.255	0.418	0.423	7.473	60	52
2014	8.325	7.128	25.413	26.882	12.037	12.161	0.208	0.027	7.405	60	52
2005	7.177	6.727	26.793	26.975	11.417	11.507	-	-	7.405	60	52
2006	4.347	7.177	24.959	26.793	11.036	11.257	0.342	0.657	3.080	60	53
2007	7.078	4.347	23.887	24.959	11.221	11.344	0.753	1.382	4.245	60	53
2008	9.776	7.078	20.577	23.887	11.028	11.093	-	-	5.116	60	53
2009	6.566	9.776	14.144	20.577	10.489	10.596	0.227	0.338	5.784	60	53
2010	4.733	6.566	15.956	14.144	11.071	11.211	0.647	1.088	6.292	60	53
2011	7.359	4.733	13.619	15.956	11.104	11.222	0.197	0.598	6.573	60	53
2012	7.411	7.359	20.640	13.619	11.338	11.493	0.313	0.108	6.887	60	53
2013	4.533	7.411	13.996	20.640	10.402	10.608	0.037	0.188	7.151	60	53
2014	4.534	4.533	25.096	13.996	10.557	10.864	0.417	0.338	7.409	60	53
2005	5.872	5.102	28.511	22.634	11.810	11.948	-	-	7.567	60	53
2006	6.008	5.872	34.662	28.511	11.341	11.560	0.543	0.812	0.000	60	54
2007	5.796	6.008	33.234	34.662	11.515	11.676	0.806	1.461	0.000	60	54
2008	8.199	5.796	29.169	33.234	11.473	11.585	0.136	0.431	0.000	60	54
2009	7.966	8.199	35.120	29.169	11.260	11.400	0.144	0.259	1.099	60	54
2010	10.640	7.966	38.051	35.120	11.359	11.461	0.564	0.999	3.209	60	54
2011	12.612	10.640	41.313	38.051	11.428	11.569	0.154	0.529	4.500	60	54
2012	18.333	12.612	42.737	41.313	11.322	11.523	0.276	0.139	5.115	60	54
2013	6.818	18.333	28.035	42.737	10.929	11.130	0.084	0.219	5.559	60	54
2014	14.824	6.818	39.047	28.035	10.897	11.172	0.164	0.051	6.111	60	54
2005	11.224	9.751	26.005	19.505	11.138	11.240	-	-	5.724	60	55
2006	10.895	11.224	28.503	26.005	10.892	10.960	0.406	0.651	6.110	60	55
2007	11.407	10.895	23.774	28.503	11.024	11.367	0.667	1.267	6.400	60	55
2008	10.312	11.407	19.223	23.774	10.927	11.140	0.057	0.317	6.477	60	55
2009	8.383	10.312	20.822	19.223	11.057	11.107	0.223	0.353	6.643	60	55
2010	9.374	8.383	29.195	20.822	11.027	11.203	0.583	1.003	6.791	60	55
							0.083	0.443			
							-	-			
							0.447	0.057			

							-	-			
2011	13.175	9.374	32.954	29.195	11.182	11.390	0.137	0.047	6.869	60	55
2012	12.314	13.175	29.289	32.954	11.253	11.277	0.383	0.283	6.997	60	55
								-			
2013	11.627	12.314	32.940	29.289	10.805	10.878	0.213	0.007	7.089	60	55
							-	-			
2014	14.343	11.627	37.335	32.940	11.074	11.147	0.177	0.387	7.165	60	55
							-	-			
2005	14.178	11.727	14.939	11.085	10.179	10.681	0.443	1.258	0.000	60.5	56
								-			
2006	7.784	14.178	15.318	14.939	9.962	10.441	0.197	0.228	0.000	60.5	56
2007	17.273	7.784	13.772	15.318	9.941	10.621	0.257	0.302	0.000	60.5	56
2008	9.212	17.273	13.373	13.772	9.643	10.029	0.527	0.962	0.000	60.5	56
2009	7.692	9.212	13.067	13.373	10.045	10.396	0.107	0.522	0.000	60.5	56
							-				
2010	10.940	7.692	16.953	13.067	9.246	9.953	0.273	0.212	0.000	60.5	56
2011	11.827	10.940	16.000	16.953	9.922	10.268	0.117	0.262	0.000	60.5	56
2012	6.225	11.827	11.291	16.000	10.209	10.537	0.417	0.432	0.000	60.5	56
							-	-			
2013	15.270	6.225	14.479	11.291	10.360	10.600	0.143	0.298	3.512	60.5	56
							-	-			
2014	7.412	15.270	16.965	14.479	10.497	10.784	0.763	0.908	4.284	60.5	56
							-	-			
2005	7.057	21.456	9.165	8.720	9.902	10.046	0.778	1.328	1.447	60	57
							-	-			
2006	10.488	7.057	13.058	9.165	9.942	10.194	0.138	0.308	1.910	60	57
2007	14.023	10.488	6.986	13.058	9.985	10.240	0.242	0.422	2.506	60	57
2008	18.318	14.023	8.866	6.986	9.071	9.090	0.582	1.022	2.773	60	57
2009	8.758	18.318	7.996	8.866	9.596	9.354	0.262	0.632	3.466	60	57
							-				
2010	4.943	8.758	11.239	7.996	9.939	9.979	0.128	0.222	4.900	60	57
2011	5.658	4.943	15.540	11.239	9.924	9.988	0.172	0.262	5.941	60	57
2012	5.476	5.658	7.368	15.540	10.225	10.338	0.412	0.302	6.458	60	57
							-	-			
2013	6.709	5.476	7.637	7.368	9.896	10.014	0.098	0.348	6.810	60	57
							-	-			
2014	6.800	6.709	13.533	7.637	9.660	10.073	0.528	0.878	7.020	60	57
							-	-			
2005	44.784	43.265	27.174	3.586	8.850	6.163	1.442	1.709	0.000	59.5	59
							-	-			
2006	68.973	44.784	1.923	27.174	8.520	4.533	0.572	0.649	0.000	59.5	59
2007	83.445	68.973	13.514	1.923	8.515	4.654	0.178	0.161	0.000	59.5	59
2008	75.068	83.445	12.376	13.514	8.592	3.638	0.938	1.121	0.000	59.5	59
2009	33.954	75.068	-	-	8.400	-	0.638	-	0.000	59.5	59
							-				
2010	27.473	33.954	-	-	8.693	-	0.092	-	0.000	59.5	59
							-				
2011	35.873	27.473	-	-	8.359	-	0.022	-	0.000	59.5	59
2012	48.208	35.873	-	-	8.736	-	0.308	-	0.000	59.5	59
2013	66.452	48.208	-	-	8.459	-	0.218	-	0.000	59.5	59
							-	-			
2014	52.578	66.452	4.593	8.900	9.336	8.581	0.152	0.559	0.000	59.5	59
							-	-			
2005	44.846	21.176	31.195	100.000	4.454	4.956	1.342	1.664	0.000	59.5	60
							-	-			
2006	18.124	44.846	56.794	31.195	6.617	5.841	0.462	0.544	0.000	59.5	60
2007	45.283	18.124	24.823	56.794	8.494	8.155	0.188	0.206	0.000	59.5	60
2008	22.381	45.283	8.696	24.823	6.862	4.956	0.858	1.106	0.000	59.5	60

2009	7.481	22.381	83.333	8.696	5.352	5.088	0.518	0.746	0.000	59.5	60
2010	35.308	7.481	-	-	5.996	-	0.122	-	0.000	59.5	60
2011	2.302	35.308	-	-	6.087	-	0.032	-	0.000	59.5	60
2012	27.322	2.302	-	-	8.684	-	0.298	-	0.000	59.5	60
2013	53.365	27.322	-	-	5.905	-	0.218	-	0.000	59.5	60
2014	16.631	53.365	-	-	6.461	-	0.122	-	0.000	59.5	60
2005	14.853	14.779	24.836	32.625	11.389	11.382	1.074	1.490	2.351	59.5	61
2006	15.007	14.853	23.202	24.836	11.197	11.162	0.294	0.420	3.332	59.5	61
2007	14.027	15.007	19.054	23.202	11.365	11.354	0.196	0.270	4.379	59.5	61
2008	15.499	14.027	21.654	19.054	11.264	11.211	0.776	1.110	5.014	59.5	61
2009	17.077	15.499	22.838	21.654	11.136	11.064	0.416	0.690	5.528	59.5	61
2010	19.261	17.077	28.096	22.838	10.904	10.787	0.134	0.230	6.143	59.5	61
2011	21.627	19.261	35.104	28.096	10.805	10.773	0.024	0.200	6.405	59.5	61
2012	24.531	21.627	29.201	35.104	10.853	10.861	0.316	0.260	6.529	59.5	61
2013	25.823	24.531	26.080	29.201	10.864	10.796	0.126	0.160	6.567	59.5	61
2014	20.496	25.823	31.495	26.080	10.708	10.655	0.304	0.690	6.277	59.5	61
2005	9.119	11.495	30.273	35.935	11.595	11.728	0.980	1.476	6.268	59.5	62
2006	10.329	9.119	27.102	30.273	11.472	11.552	0.170	0.366	6.495	59.5	62
2007	11.513	10.329	23.229	27.102	11.511	11.651	0.270	0.374	6.600	59.5	62
2008	9.324	11.513	21.458	23.229	11.584	11.717	0.760	1.174	6.604	59.5	62
2009	11.760	9.324	17.906	21.458	11.441	11.416	0.330	0.694	6.659	59.5	62
2010	14.556	11.760	21.406	17.906	11.419	11.446	0.200	0.204	6.628	59.5	62
2011	16.436	14.556	21.920	21.406	11.568	11.633	0.010	0.144	6.536	59.5	62
2012	13.909	16.436	22.455	21.920	11.726	11.757	0.320	0.204	6.368	59.5	62
2013	13.743	13.909	22.191	22.455	11.387	11.407	0.090	0.186	6.078	59.5	62
2014	13.878	13.743	25.656	22.191	11.209	11.290	0.410	0.766	5.899	59.5	62

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684 Supplementary Table 2. Average annual growth rate of log-transformed perch and
685 pikeperch CPUE values during 2005–2014 and maximum breeding cormorant
686 numbers during 2003–2012 in ICES grids. Significant coefficients are bolded.

ICES	Perch	Pikeperch	Cormorant max
2	0.111 ± 0.020	0.022 ± 0.047	0
6	0.054 ± 0.026	-0.004 ± 0.044	240
7	0.096 ± 0.024	0.123 ± 0.040	47
11	0.043 ± 0.041	0.080 ± 0.070	4
12	-0.062 ± 0.032	-	0
15	0.054 ± 0.037	0.185 ± 0.114	0
19	0.035 ± 0.027	-0.048 ± 0.058	4
22	0.129 ± 0.080	-	0
23	0.070 ± 0.015	0.122 ± 0.068	83
24	0.105 ± 0.022	-0.042 ± 0.065	0
27	0.093 ± 0.026	-	0
28	-0.000 ± 0.020	-0.016 ± 0.103	110
32	0.034 ± 0.027	0.163 ± 0.062	40
37	0.013 ± 0.034	0.058 ± 0.023	3981
42	-0.017 ± 0.038	-0.114 ± 0.043	3426
47	0.045 ± 0.038	-0.018 ± 0.025	1654
49	0.087 ± 0.019	-0.007 ± 0.029	0
50	0.074 ± 0.025	-0.025 ± 0.044	56
51	0.068 ± 0.042	-0.001 ± 0.038	1389
52	-0.032 ± 0.017	-0.029 ± 0.016	2179
53	-0.029 ± 0.031	-0.039 ± 0.028	2437

54	0.100 ± 0.033	0.023 ± 0.016	629
55	0.024 ± 0.016	0.044 ± 0.019	1519
56	-0.031 ± 0.039	0.003 ± 0.015	156
57	-0.074 ± 0.043	0.012 ± 0.033	1264
59	-0.024 ± 0.043	-	0
60	-0.056 ± 0.111	-	0
61	0.064 ± 0.012	0.041 ± 0.016	925
62	0.052 ± 0.014	-0.017 ± 0.016	879

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